

A Revision of the Genus *Benthovoluta* with Notes on the Evolution of the Subfamily Ptychatractinae (Prosobranchia: Turbinellidae)

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ABSTRACT

The genus *Benthovoluta* Kuroda and Habe, 1950 is revised and restricted to four Recent species: *B. hilgendorfi* (von Martens, 1897); *B. gracilior* Rehder, 1967; *B. krigei* Kilburn, 1971; and *B. claydoni* new species. Phenetic analyses using morphometric data indicate that the three eastern Indian-western Pacific species are more closely related to each other than any is to the single species from the western Indian Ocean. Further phenetic analyses suggest that *Benthovoluta* is most closely related to the genus *Surculina* from off New Zealand and the eastern Pacific, that both are more remotely related to the small-shelled genera *Cyomesus*, *Metzgeria*, and *Ptychatractus*, all restricted to the Northern Hemisphere, and that the genera *Ceratoxancus* and *Latiromitra* are most distantly related, and may not belong to the family Turbinellidae. Dissections of *Benthovoluta claydoni* revealed that the mantle cavity and alimentary and male reproductive systems resemble those of the subfamily Turbinellinae, while the female reproductive system more closely resembled those of Vasiniae and Columbariinae. A short, stout proboscis, as well as the presence of an amphipod carapace and lack of polychaete setae in the posterior alimentary canal, suggest a diet and mode of feeding that differ from those of other Turbinellidae. These dissections represent the first anatomical data for any species attributed to the subfamily Ptychatractinae. Cladistic analyses of anatomical characters reveal that the Ptychatractinae are most closely related to the Turbinellinae, and that the Vasiniae are most distantly related to the other members of the family Turbinellidae.

INTRODUCTION

The genus *Benthovoluta* comprises a small, poorly known group of fusiform turbinellid gastropods that inhabit the bathyal zone along the margins of the Indian and Pacific oceans. Records are few, and the taxonomic position of the genus, as well as the often ephemeral inclusion of species within it, have been based on shell and occasionally on radular characters. Reports of fossil representatives are rare, tentative, and limited to Late Tertiary (Miocene or Pliocene) deep water deposits along the

northwestern Pacific (Yokoyama, 1920; Taki & Oyama, 1954; MacNeil, 1960).

Kuroda and Habe (1950) erected the genus *Benthovoluta* within the family Volutidae, and designated *Phenacoptygma? kiensis* Kuroda, 1931, a Recent species originally proposed with some doubt as a turrid, as type. These authors also included the Pliocene "*Mitra*" *plicifera* Yokoyama, 1920 (*non Mitra plicifera* S. V. Wood, 1848) in *Benthovoluta*, but placed both these taxa in the synonymy of *Voluta hilgendorfi* von Martens, 1897 in the same publication. On the basis of a figure of the radula of *B. hilgendorfi*, published without comment by Habe (1952), Kuroda (1965) transferred this genus to the family Turbinellidae and suggested affinities with the genera *Metzgeria* Norman, 1879 and *Ceratoxancus* Kuroda, 1952. Rehder (1967) noted similarities between the shell and radular morphologies of *Benthovoluta* and those of *Surculina* Dall, 1905, *Ptychatractus* Stimpson, 1865, and, more remotely, the fusiform species of *Turbinella* Lamarck, 1799. In the same paper, Rehder synonymized *Phenacoptygma* Dall, 1918 under *Surculina*.

Cernohorsky (1973) used Stimpson's (1865) family group name Ptychatractidae, previously placed in the synonymy of Turbinellidae by most authors, as a subfamily within Turbinellidae to include the five genera mentioned above. Quinn (1981) proposed the genus *Cyomesus* for a number of small-shelled species that had been referred to *Benthovoluta* by Cernohorsky (1973), and suggested that the Upper Cretaceous genera *Mesorhythis* Meek, 1876, *Paleofusimitra* Sohl, 1963, and *Mitrodomus* Sohl, 1963 as well as the Eocene genus *Fusimitra* Conrad, 1855 might also belong to the subfamily Ptychatractinae. Based on shell morphology, Bouchet and Waren (1985) referred the monotypic, eastern Atlantic, bathyabysal genus *Latiromitra* Locard, 1897 to the family Turbinellidae, and considered *Cyomesus* a synonym.

Deep-water trawling off northwestern Australia by the Australian Commonwealth Scientific and Industrial Organization (CSIRO) as well as by commercial fishermen

has yielded a number of specimens, including several with preserved soft parts, of a new species of *Benthovoluta* that is described herein. This description includes the first account of the anatomy of any species attributed to the subfamily Ptychactractinae. The known species of *Benthovoluta* are reviewed and the phylogenetic affinities of this genus, and by inference the subfamily, are discussed.

MATERIALS AND METHODS

Specimens for anatomical studies were cracked in a vice, the loose shell fragments removed, and soft parts placed in 20% hydrochloric acid (HCl), to dissolve the remaining shell. Soft parts were rinsed in distilled water and returned to 70% ethanol for dissection.

Sections for analysis of shell ultrastructure were cut using a diamond saw. Some sections were broken to expose fracture surfaces, others polished and etched for a few seconds with 1% HCl. Radulae for SEM examination were critical point dried. In order to determine gut contents, the posterior esophagus, stomach, intestine, and rectum of three specimens of *Benthovoluta claydoni* were excised, transferred to a microscope slide, teased apart, and examined. Several drops of bleach (5% sodium hypochlorite, NaOCl) were then added to dissolve organic matter. After 20 minutes, the sample was diluted with distilled water, filtered through a 0.45 μm membrane filter, rinsed, dried, and examined under SEM. Scanning electron micrographs were taken using a Hitachi S-570 SEM.

The specimens of *Benthovoluta* listed in the material examined sections, as well as the published figure of the holotype of *B. krigei* (Kilburn, 1971: fig. 3a) were scored for the 12 characters listed in table 1. Analyses of relationships between species of *Benthovoluta* were confined to shell characters, as anatomical data were available for only one species, and published line drawings of the radulae of two other species lacked sufficient detail to ascertain differentiating characteristics. The mean values of the characters comprised the data matrix for phenetic analyses. To investigate the relationships between the Recent genera attributed to Ptychactractinae, specimens or figures of their type species (listed in table 2) were chosen to serve as exemplars, and scored for the characters listed in table 3. These values formed the data matrix used in a second series of phenetic analyses. Finally, the phylogenetic relationships between the four subfamilies of Turbinellidae were investigated using the taxa listed in table 4 as exemplars of their subfamilies, and scoring them for anatomical characters listed in table 5. Characters were polarized based on Ponder's (1973) analysis of the evolution of organ systems in Neogastropoda.

Morphometric shell characters [tables 1, 2 (characters 1-9)] were determined using CONCH version 1.0 (Chapman *et al.*, 1987). For phenetic analyses, the data were standardized (mean = 0, standard deviation = 1), a Euclidian distance matrix calculated, and phenograms based

Table 1. Shell characters used in phenetic analyses of relationships between the species of *Benthovoluta*. Characters 1 through 5 describe the geometry of the generalized shell form (Harasewych, 1982).

- | |
|---|
| 1) Shape of the generating curve of the body cavity (Slc) |
| 2) Shape of the generating curve of the siphonal canal (Ssc) |
| 3) Relative siphonal length (Rsl) |
| 4) Siphonal angle (beta) |
| 5) Angle of generating curve (theta) |
| 6) Rate of whorl expansion (W) |
| 7) Position of generating curve relative to axis (D) |
| 8) Rate of whorl translation (T) |
| 9) Aperture + siphonal canal length/shell length (A + SCL/SL) |
| 10) Color pattern (CP): solid (0), banded (1) |
| 11) Suture (Sut): adpressed (0), abutting (1) |
| 12) Surface sculpture on body whorl (Sculp): incised spiral furrows (0), spiral cords (1), cancellate (2) |

on UPGMA and single linkage (nearest neighbor) clustering algorithms produced using SYSTAT version 3.4 (Wilkinson, 1986). Cladistic analyses were run using PAUP version 2.4 (Swofford, 1985).

Repositories of examined specimens are indicated by the following abbreviations:

DMNH	Delaware Museum of Natural History
USNM	National Museum of Natural History, Smithsonian Institution
SAM	South African Museum
WAM	Western Australian Museum

SYSTEMATICS

Family Turbinellidae Swainson, 1840

This family is best known for its large, tropical, heavy-shelled, shallow-water species that comprise the low diversity subfamilies Turbinellinae and Vasiniae. The bathyal subfamilies Columbariinae and Ptychactractinae are far more diverse and widely distributed, ranging from equatorial to polar latitudes. Species belonging to the latter two subfamilies tend to be significantly smaller and thinner-shelled. Characteristic features of the family include fusiform to biconical shells consisting of two or three layers of crossed-lamellar aragonite, bulbous protoconchs, open, axially-oriented siphonal canals, and columellae that usually have two to four spiral folds. Opercula are elongate and terminally nucleate. Animals generally have a long narrow proboscis, a small radular ribbon with tricuspid rachidian and mono- or bicuspid lateral teeth, an open or partially fused sperm groove, and lack accessory salivary glands. Diets consist mostly or exclusively of polychaetes (Hornell, 1914; Moses, 1923; Harasewych, 1983, 1986) sipunculids (Taylor *et al.*, 1980), and "worms" (Bandel, 1984).

Subfamily Ptychactractinae Stimpson, 1865

As taxa have been assigned to this, the most poorly known subfamily in Turbinellidae, exclusively on the basis of

Table 2. Recent genera attributed to the subfamily Ptychactinae and their type species. Specimens or figures that provided characters for phenetic analyses are listed.

Benthovoluta Kuroda and Habe, 1950
Benthovoluta hilgendorfi (von Martens, 1897), USNM S24942, off Choshi, Japan (figure 1, herein; radula Rehder, 1967: fig. 11)

Ceratoxancus Kuroda, 1952
Ceratoxancus teremachii Kuroda, 1952, off Tosa, Japan (Shikama 1963: pl. 76, fig. 4, radula unknown)

Cyomesus Quinn, 1981
Cyomesus meckianus (Dall, 1889), lectotype, USNM 86970, BLAKE station 100, off Moro Light, Cuba 732 m (Quinn, 1981: fig. 1; radula Bayer, 1971: fig. 55D)

Latiromitra Locard, 1897
Latiromitra cryptodon (P. Fischer, 1852), MNHN, off Morocco, 1900 m (Bouchet & Waren, 1985: fig. 676; radula unknown)

Metzgeria Norman, 1879
Metzgeria albus (Jeffreys, 1873), INGOLF station 32, Davis Strait, western Greenland (Bouchet & Waren, 1985: fig. 677; radula fig. 393)

Ptychactractus Stimpson, 1865
Ptychactractus ligatus (Mighels and Adams, 1842), USNM 414668, off Eastport, Maine, in 18 m (unpublished photograph of shell; radula figure 19, herein)

Surculina Dall, 1908
Surculina blanda (Dall, 1980), holotype, USNM 123119, off Cocos Island, Gulf of Panama in 1951 m (Rehder, 1967: fig. 7; radula fig. 10).

shell and radular morphology, assumptions of monophyly for this group are, at best, tentative. Shells are fusiform, high-spired, and small (rarely exceeding 100 mm), with elongate, narrow apertures and zero to four, strong to weak columellar teeth. Radulae have tricuspid rachidian and monocuspid lateral teeth. Most members of this subfamily inhabit the bathyal zone, with some species occurring at depths in excess of 2,000 m. A number of the boreal species, including the type species of the type genus of the subfamily, have been taken in less than 20 m.

Genus *Benthovoluta* Kuroda and Habe, 1950

Benthovoluta Kuroda and Habe, 1950:37. Type species by original designation *Phenacoptygma*? *kiensis* Kuroda, 1931; is *Voluta hilgendorfi* von Martens, 1897.

Although 10 Recent species, including one described herein, have been attributed to *Benthovoluta* (Shikama, 1971; Cernohorsky, 1973; Habe, 1976), this genus is here restricted to the four species discussed below. Characteristic features of the genus include comparatively large shells with long siphonal canals, rachidian teeth with cusps limited to the central half of the tooth, and broad-

Table 3. Shell and radular characters used in phenetic analyses of relationships between Recent genera attributed to the subfamily Ptychactinae. Characters 1 through 8 describe the geometry of the generalized shell form (Harasewych, 1952).

- 1) Shape of the generating curve of the body cavity (Sbc)
- 2) Shape of the generating curve of the siphonal canal (Ssc)
- 3) Relative siphonal length (Rsl)
- 4) Siphonal angle (beta)
- 5) Angle of generating curve (theta)
- 6) Rate of whorl expansion (W)
- 7) Position of generating curve relative to axis (D)
- 8) Rate of whorl translation (T)
- 9) Aperture + siphonal canal length/shell length (A + SCL/SL)
- 10) Protoconch (Prot): multispiral (0); paucispiral (1)
- 11) Lateral radular teeth (Lat): single cusp emanating from outer edge of basal plate (0); base of single cusp spanning all or most of the basal plate (1)
- 12) Rachidian teeth with cusps spanning (Rach1): > 0.5 basal plate (0); < 0.5 basal plate (1)
- 13) Rachidian teeth with basal plate (Rach2): broad, curved (0); narrow, recurved (1)

based, trowel-like lateral teeth. The remaining species are referred to the genus *Cyomesus* Quinn, 1981, which may be readily distinguished from *Benthovoluta* on the basis of its much smaller shell, with shorter siphonal canal and proportionally higher spire, and a radular ribbon in which the rachidian teeth are stouter, with larger, broader cusps, and lateral teeth that are narrow, long, and scythe-shaped.

Benthovoluta hilgendorfi (von Martens, 1897) (figures 1–3)

Voluta hilgendorfi von Martens, 1897:176, pl. 17, fig. 1.

?*Mitra plicifera* Yokoyama, 1920:48, pl. 2, figs. 16a,b; Hatai and Nishiyama, 1952:215; Taki and Oyama, 1954: pl. 3, figs. 16a,b; Cernohorsky, 1972:223 (*non Mitra plicifera* S. V. Wood, 1848).

Phenacoptygma? *kiense* Kuroda, 1931:48, fig. 1

Benthovoluta hilgendorfi (von Martens) Kuroda and Habe, 1950:37, pl. 5, fig. 2, Kira, 1962:92, pl. 33, fig. 3; Shikama, 1963:97, pl. 79, fig. 7; Kuroda, 1965:50; Cernohorsky, 1973: t26–127 (in part).

Description: Shell (figures 1, 2) to 84 mm, solid, elongate, fusiform. Protoconch (figure 3) of $\frac{3}{4}$ whorl, smooth, deflected from coiling axis. Transition to teleoconch abrupt, marked by thickened protoconch lip and first appearance of spiral threads and axial ribs. Teleoconch with up to 10 convex, rounded whorls. Suture adpressed. Shoulder rounded. Spiral sculpture of incised spiral lines, 37–45 on body whorl, 9–11 on exposed portions of previous whorls, and 20–27 on siphonal canal. Incised lines may be thinner and shallower along siphonal canal. Axial sculpture of 12–14 costae, prominent on early whorls, rarely occurring beyond 8th postnuclear whorl. Aperture elongate, elliptical. Outer lip smooth, thin, porcellaneous. Inner lip smooth, glazed. Columella solid, with 3 (oc-

Table 4. Species and specimens that provided anatomical data for cladistic analyses of relationships between the subfamilies of Turbinellidae.

Columbariinae Tomlin, 1928
<i>Coluzca rotunda</i> (Barnard, 1959), 2 ♀, 2 ♂, SAM A 4592, off Cape Town, South Africa, 1,006–869 m
Ptychactractinae Stimpson, 1865
<i>Benthovoluta claydoni</i> new species, data contained herein
Turbinellinae Swainson, 1840
<i>Turbinella angulata</i> (Lightfoot, 1786), 2 ♀, 2 ♂, USNM 846315, off Carrie Bow Cay, Belize, 1–2 m
Vasinae H. and A. Adams, 1853
<i>Vasum muricatum</i> (Born, 1778), 2 ♀, 2 ♂, USNM 846316, off Carrie Bow Cay, Belize, 1–2 m

asionally 4) simple folds. Central fold most prominent, may become fused with anteriormost fold. Siphonal canal broad, tapers distally, crosses coiling axis. Interior shell surfaces smooth, except for columellar folds. Color chestnut brown. Early whorls may be lighter. Aperture may have a whitish overglaze. Operculum reduced, thin, elongate, with terminal nucleus. Soft parts other than radula are unknown. The radula was figured by Habe (1952) and refigured by Rehder (1967).

Type locality: Von Martens (1897:176) gave the locality as "Japan, probably from Hakodate, Hilgendorf". This is outside the range of the species, as reported by several Japanese authors (e.g., Kira, 1962:92; Kuroda *et al.*, 1971:199), and probably in error.

Material examined: USNM 605772, Tosa, Japan, 274 m; USNM 612610, Japan; USNM 824942, off Choshi, Japan.

Distribution: Off the eastern coast of Japan, south of Choshi (Central Honshu), in 50–300 m.

Ecology: This species inhabits sandy bottoms at depths of 50–300 m. Most specimens examined had one or more repaired breaks, indicating unsuccessful predation by crabs and/or fish.

Remarks: This species is readily identified on the basis of its chestnut brown color and its spiral sculpture of incised furrows.

Benthovoluta gracilior Rehder, 1967
(figures 4–6)

Benthovoluta gracilior Rehder, 1967:185, figs. 5, 6; Cernohorsky, 1973:129.

Description: Shell (figures 4, 5) to 57 mm, thin, biconical, narrowly fusiform. Protoconch (figure 6) of $\frac{3}{4}$ whorl, smooth. Transition to teleoconch demarcated by abrupt appearance of axial costae and spiral threads. Teleoconch with up to 10 $\frac{3}{4}$ whorls. Suture adpressed. Shoulder pronounced, rounded. Spiral sculpture of 42–46 fine cords

Table 5. Characters and character states used in cladistic analyses of the relationships between the subfamilies of Turbinellidae.

1) Siphon, long. exposed (a); narrow, covered (b); broad, fleshy, covered (c)
2) Median cephalic furrow. absent (a); present (b)
3) Retracted proboscis: linear (a); folded (b)
4) Proboscis retractor muscles: paired (a); single (b)
5) Lateral radular teeth: bicusped (a); monocusped (b)
6) Rachidian teeth with cusps spanning: > 0.75 basal plate (a); < 0.75 basal plate (b)
7) Anal gland. present (a); absent (b)
8) Bursa copulatrix: present (a); absent (b)
9) Sperm groove: along inner lateral edge of penis (a); runs ventrally just prior to opening (b)
10) Penial papilla: absent (a); present (b)

on body whorl, 48–52 on siphonal canal, and 16–18 on exposed portions of earlier whorls. Fine spiral threads may occur between adjacent cords, especially between shoulder and suture. Axial sculpture of 16–18 prominent costae per whorl. Axial costae poorly defined below mid-point of body whorl. Aperture elongate, narrow. Outer lip thin, smooth. Columella solid, with 2 folds, posterior fold more prominent. Siphonal canal long, narrow, crosses coiling axis. Periostracum thin, of straw-colored axial blades. Operculum and soft parts unknown.

Type locality: Off Cagayan Islands, north Sulu Sea, Philippines, 9°38'30"N, 121°11'E, in 929 m. "Albatross I" sta. 5423.

Material examined: USNM 637252 (holotype), USNM 238408 (4 paratypes), DMNH 15456 (paratype), all from the type locality.

Distribution: Known only from the type locality.

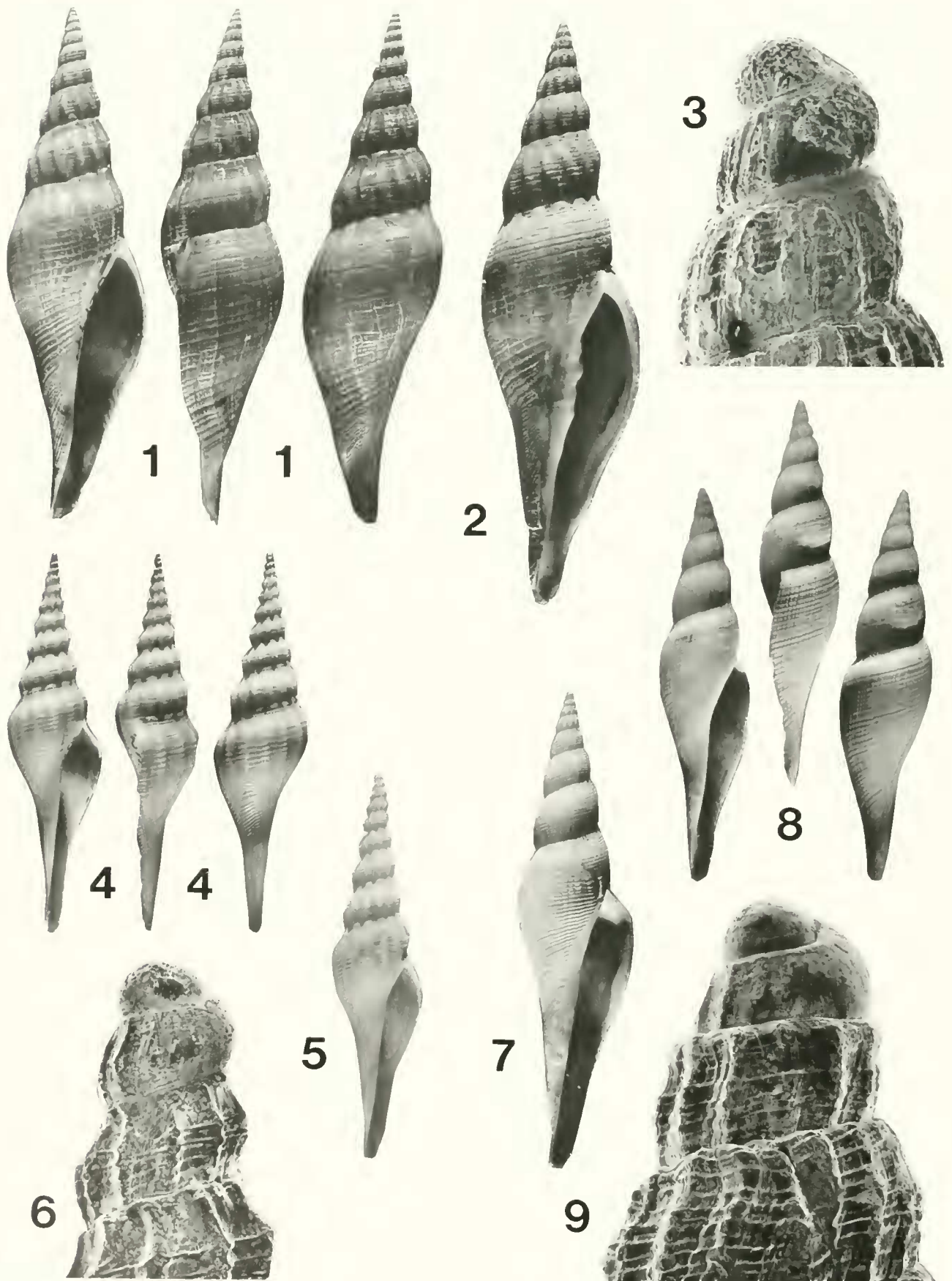
Ecology: This species was taken in 929 m on gray mud and coral sand bottom.

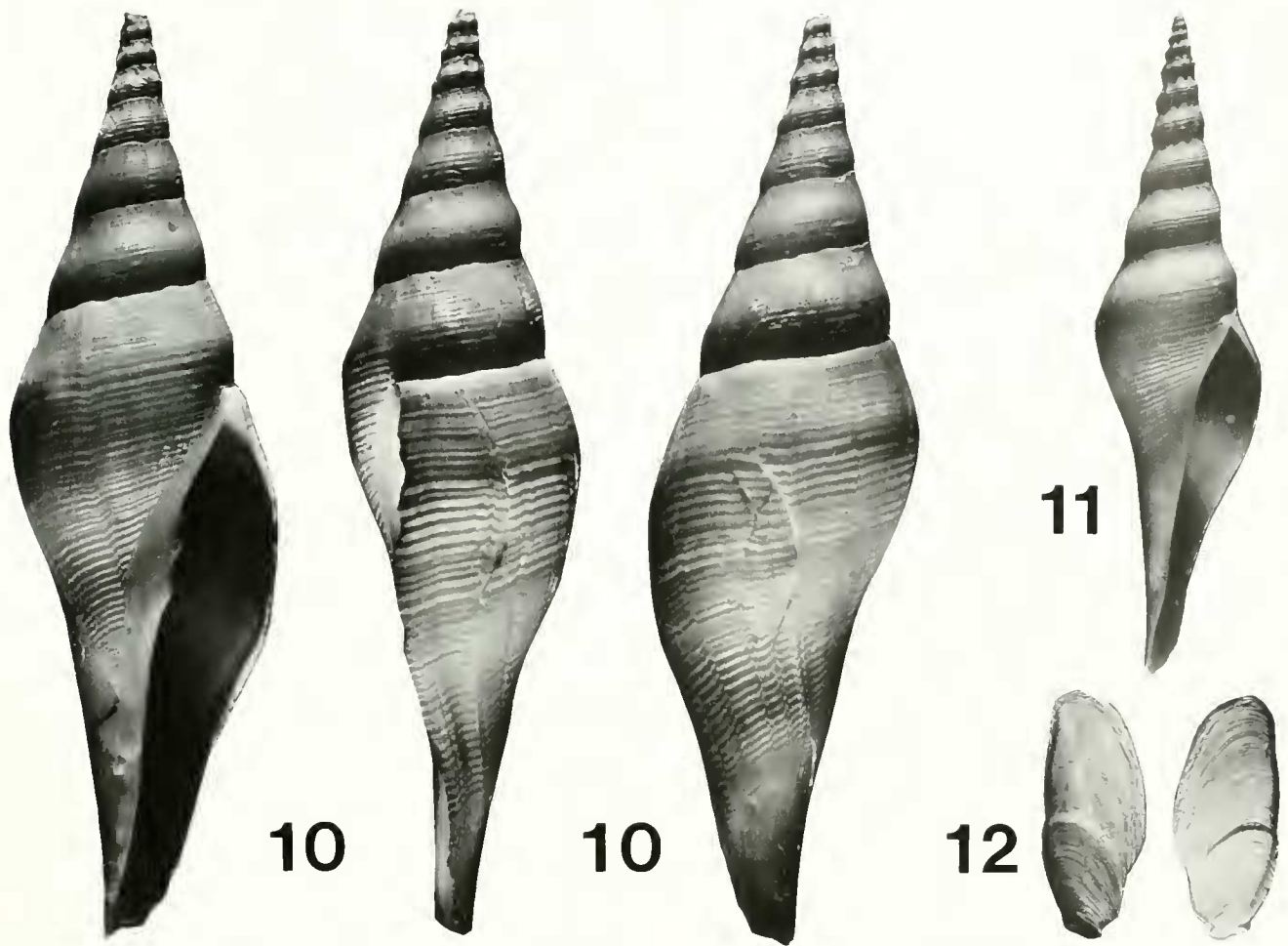
Remarks: This species differs from its congeners in having a smaller, thinner, more highly spired shell, with axial ribs that are prominent on the body whorl. It has only been taken once, and at twice the depth inhabited by its known congeners.

Benthovoluta krigei Kilburn, 1971
(figures 7–9)

Benthovoluta krigei Kilburn, 1971:127–130, figs. 2d, 3a,b; Kensley, 1973:180, fig. 686.

Description: Shell (figures 7, 8) to 71 mm, solid, inflated, narrowly fusiform. Protoconch (figure 9) of $\frac{3}{4}$ whorl, smooth, globose, deviated from coiling axis. Transition to teleoconch marked by abrupt appearance of numerous fine spiral threads and strong axial ribs. Teleoconch with up to 9 $\frac{3}{4}$ convex, rounded whorls. Suture strongly adpressed in early whorls, whorls abutting in larger specimens. Shoulder weak, rounded. Spiral sculpture of broad,





Figures 1-3. *Benthovoluta hilgendorfi* (von Martens, 1897). **1.** USNM 824942, off Choshi, Japan. **2.** USNM 605772, Tosa, Japan, in 274 m. **3.** Protoconch of specimen in figure 1. **Figures 4-6.** *Benthovoluta gracilior* Rehder, 1967. **4.** Holotype, USNM 637252. **5.** Paratype, USNM 238408, both from off Cagayan Islands, northern Sulu Sea, Philippines, in 928 m. **6.** Protoconch of specimen in figure 5. **Figures 7-9.** *Benthovoluta krigei* Kilburn, 1971. **7, 8.** USNM 824943, off Inhaca Island, Mocambique, trawled in 475 m. **9.** Protoconch of specimen in figure 7.

Figures 10-12. *Benthovoluta claydoni* new species. **10.** Holotype, WAM 3252-83. **11.** Paratype 1, USNM 862217, both from SW of Imperieuse Reef, Rowley Shoals, Western Australia, 400-401 m. **12.** Operculum of holotype, left—inner surface, right—outer surface. All shells 1.25 ×, protoconchs 30.0 ×, operculum 3.0 ×.

rounded, closely-spaced cords that give shell surface a deeply incised appearance, 36-48 on body whorl, 20-23 on penultimate whorl, 13-19 on siphonal canal. Axial sculpture of 12-16 costae, prominent on early whorls, becoming reduced and generally absent by 6th postnuclear whorl. Aperture elongate, narrow. Outer lip thin, strongly sinuate posteriorly. Inner lip smooth, with shell surface dissolved to below level of spiral sculpture. Columella solid, folds weak or lacking. Siphonal canal long, broad, distally tapering. Interior shell surfaces smooth. Color light tan, with darker brown between suture and shoulder, along the anterior half of the body whorl, distal portion of the siphonal canal, and in a thin band along the margin of the outer lip. Periostracum unknown. Operculum as in *B. hilgendorfi* (fide Kilburn, 1971).

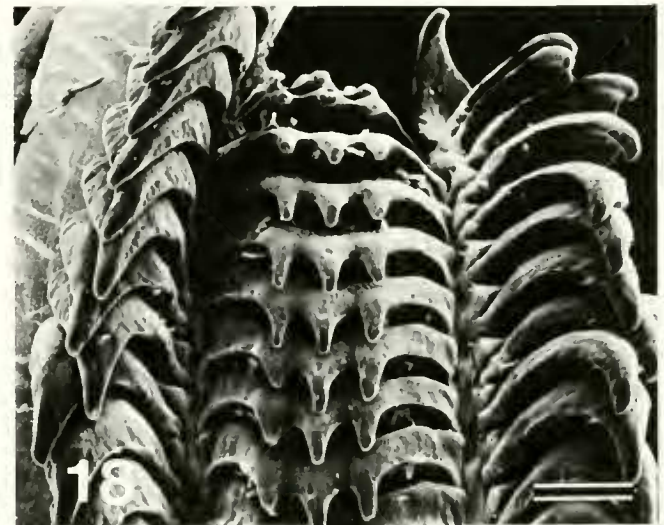
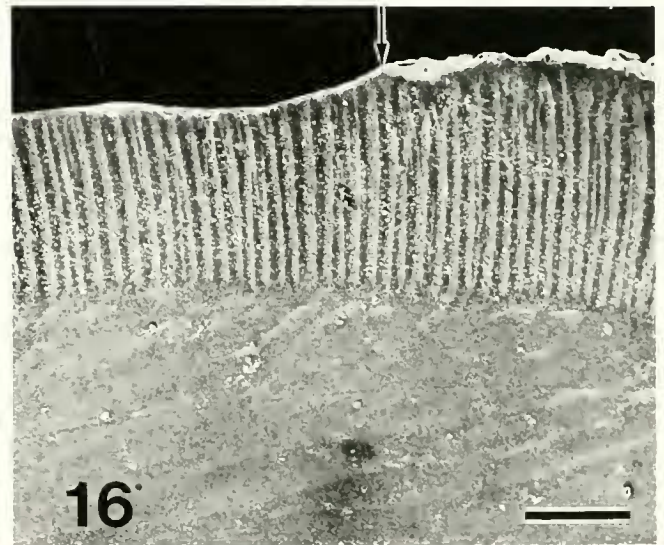
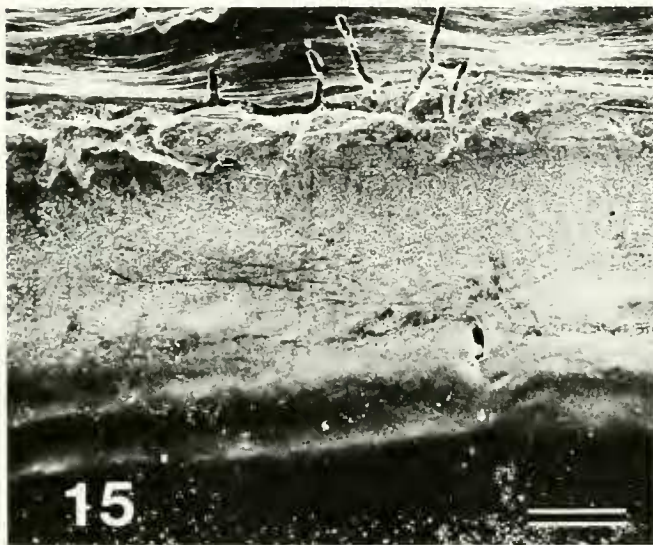
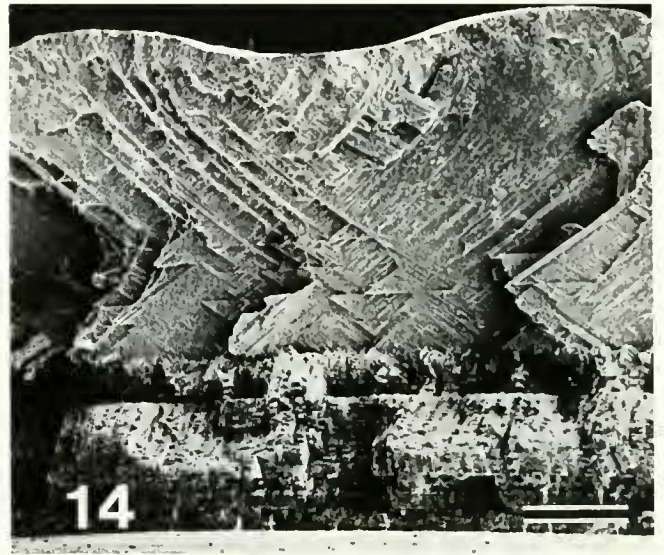
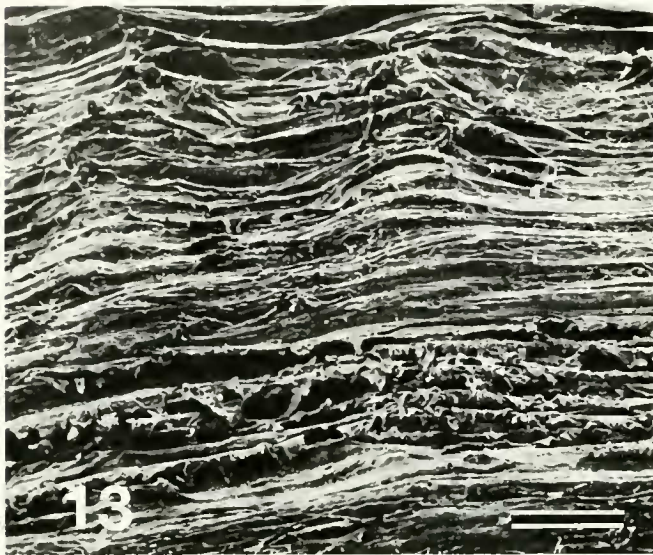
Kilburn (1971:129) described the animal as white, with thin, filiform tentacles with eyes at the outer sides of their bases. Radula (Kilburn, 1971:129, fig. 2d) with 69 rows of teeth. Rachidian teeth tricuspid, with broad, arcuate base. Lateral teeth monocuspid, claw-like.

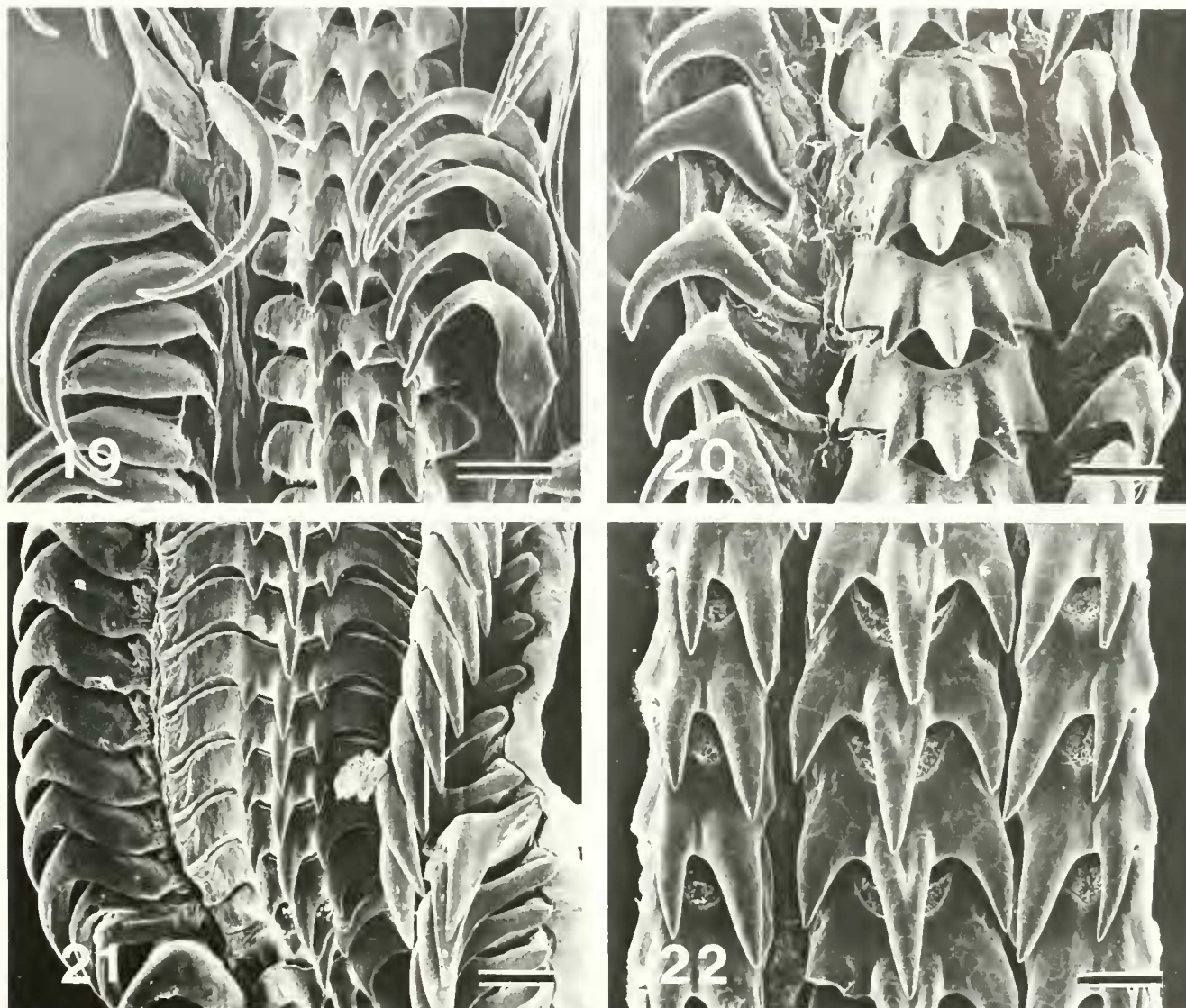
Type locality: 80 km due east of Inhaca Island, Mocambique, in 512 m (280 fm).

Material examined: USNM 824943, off Inhaca Island, Mocambique, in 475 m.

Distribution: This species has only been taken off Inhaca Island, Mocambique at depths of 475-512 m.

Remarks: Kilburn (1971:129) considered this species to more closely resemble *Surculina* than any species of *Ben-*





Figures 13–18. *Benthovoluta claydoni* new species. **13.** Periostracum, scale bar = 300 μm . **14.** Shell ultrastructure, fracture surface parallel to growing edge, scale bar = 200 μm . **15.** Parietal area of columella, showing reabsorption of portion of outermost shell layer, scale bar = 100 μm . **16.** Section through columella perpendicular to shell axis, surface polished and acid-etched (1% HCl). Arrow indicates limit of shell reabsorption, scale bar = 200 μm . **17.** Rachidian teeth, scale bar = 30 μm . **18.** Radular ribbon, scale bar = 50 μm .

Figure 19. Radular ribbon of *Ptychotractus ligatus* (Mighels and Adams, 1842), scale bar = 30 μm . **Figure 20.** Radular ribbon of *Cyomesus chaunax* (Bayer, 1971), scale bar = 20 μm . **Figure 21.** Radular ribbon of *Turbinella pyrum* (Linné, 1758), scale bar = 30 μm . **Figure 22.** Radular ribbon of *Vasum muricatum* (Born, 1775), scale bar = 50 μm .

thovoluta in shell morphology, but assigned it to the latter genus because Dall (1908:292) reported that *Surculina cortczi* (Dall, 1908) lacked eyes, tentacles, and operculum, and due to a misinterpretation of Rehder's (1967: fig. 10) figure showing two views of a monocuspid lateral tooth as a bicuspid lateral tooth. Although the relationship between *Benthovoluta* and *Surculina* bears closer investigation when anatomical material becomes available, *Benthovoluta krigei* is more closely related to its Indo-Pacific congeners than to any species of *Sur-*

culina. Examination of additional specimens of *B. krigei* revealed that several had weak but nevertheless distinguishable columellar folds corresponding to the anteriormost two folds of *B. hilgendorfi*.

Benthovoluta claydoni new species
(figures 10–18, 23–26; table 6)

Description: Shell (figures 10, 11) to 101 mm, solid, elongate, fusiform. Protoconch broken or abraded on all

Table 6. *Benthovoluta claydoni* new species. Measurements of shell characters. Linear measurements in mm

Character	\bar{x}	Range	SD
Shell length (SL)	85.0	62.2–100.9	9.4
Aperture + siphonal canal length (A + SCL)	51.0	35.2–60.3	6.6
A + SCL/SL	0.599	0.566–0.622	0.018
# Whorls	10.3	8–13	1.4
Spire angle	29 t	25.5–32.0	2.4

specimens examined. Teleoconch with up to 13 slightly convex whorls. Suture adpressed. Shoulder somewhat pronounced on early whorls, becoming more rounded with increasing size. Spiral sculpture of weak, simple cords, 33–42 on body whorl, 12–18 on exposed portions of earlier whorls, 15–35 on siphonal canal. Cords strongest between shoulder and siphonal canal, weakest at suture and distal portion of siphonal canal. Axial sculpture of 9–11 costae, most pronounced on earlier whorls, becoming reduced and usually absent by 7th postnuclear whorl. Aperture elongate, elliptical. Outer lip smooth, thin, porcellaneous. Inner lip smooth, characterized by dissolution of portion of outermost shell layer from parietal region (figures 15, 16). Columella solid, with 3 simple folds, central fold most prominent, posteriormost fold weakest and sometimes absent. Siphonal canal broad, long, crosses coiling axis. Interior shell surfaces uniformly smooth, unmodified except by columellar folds. Periostracum (figure 13) of short, thin, straw-colored, axial blades. Operculum (figure 12) greatly reduced ($< 0.4 \times$ aperture length), thin, elongate, terminally nucleated.

Ultrastructure: Shell of two orthogonal layers of crossed-lamellar aragonite (figure 14). Outer layer, 420–620 μm thick, with crystal faces colabrally aligned. Inner layer, 320–350 μm thick, with crystal faces perpendicular to growing edge. Spiral sculpture limited to outer layer, columellar folds comprised of inner layer. Portion of outer layer along parietal area dissolved to below level of spiral sculpture (figures 15, 16), indicating boundary of inner lip.

External anatomy: Soft parts comprise $4\frac{1}{2}$ whorls. Mantle cavity extends over 1 whorl, kidney spans $\frac{1}{2}$ whorl, digestive gland $2\frac{1}{2}$ whorls. Foot short, narrow ($L/W = 2.0$), squarish anteriorly, rounded posteriorly. Operculum as broad as foot. Preserved animals khaki tan in color, lack discernible color pattern. Siphon broad, muscular, simple. Head small, narrow, with long tentacles (figure 25, t) that have large, black eyes (figure 25, e) at their outer bases.

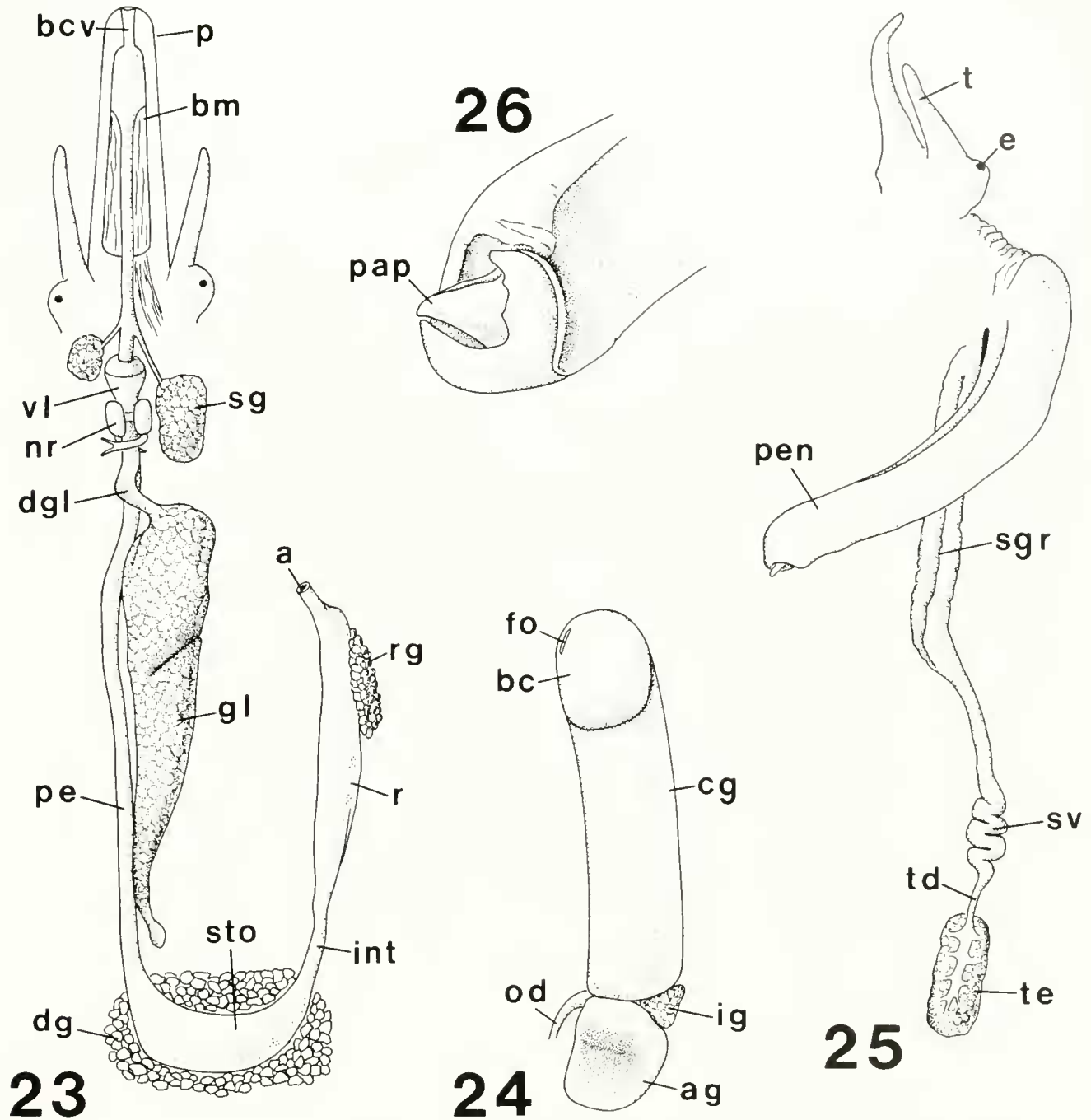
Mantle cavity: Mantle cavity organs similar to those of *Fulgurofusus brayi* (Clench, 1959), as described by Harszewych (1983). Mantle edge slightly thickened, finely papillose. Osphradium large, long ($L/W = 4.3$), consisting of about 70 triangular filaments above and 60 below the axis. Ctenidium of about 200 deep hanging leaflets, $1.9 \times$ as long and $1.0 \times$ as wide as osphradium. Hy-

pobranchial gland transversely pleated, deeply glandular, unpigmented. Rectum and genital ducts along right side of mantle cavity, large pericardium and kidney along its back wall.

Alimentary system: Rhynchostome opens at base of tentacles, leads to short, muscular, pleurembolic proboscis (figure 23, p). Single, large proboscis retractor muscle attaches to right wall of cephalic hemocoel and surrounds a large blood vessel. Buccal cavity (figure 23, bev) deep, with strong longitudinal folds, lacks jaws. Buccal mass (figure 23, bm) large, muscular, projects beyond rear of retracted proboscis. Radular sack short, contained within buccal mass. Radular ribbon (figure 18) short (4 mm), narrow (300 μm), contains 88–97 rows of teeth ($n = 3$). Rachidian teeth (figure 17) with three cusps emanating from middle half of tooth. Basal plate recurved, narrow. Lateral teeth with single, trowel-like cusp. Esophagus runs anteriorly from rear of proboscis, expanding to form large valve of Leiblein (figure 23, vl) before passing through nerve ring. Salivary glands (figure 23, sg) asymmetrical, situated at rear of retracted proboscis. Ducts from salivary glands join esophagus just anterior to the valve of Leiblein, become embedded beneath the dorsal folds. Accessory salivary glands absent. Between nerve ring and duct from gland of Leiblein (figure 23, dgl), esophagus expands and becomes glandular, resembling a “glande framboisee” (Fretter & Graham, 1962:216). Gland of Leiblein (figure 23, gl) large, brownish, broad anteriorly, tapering posteriorly to form blind ampulla, fills posterior half of cephalic hemocoel. Posterior esophagus (figure 23, pe) runs along left side of gland of Leiblein, expanding along anterior face of digestive gland (figure 23, dg) to form stomach. Stomach (figure 23, sto) U-shaped, with small caecum, prominent typhlosoles. Duct from digestive gland enters near esophageal opening. Intestine (figure 23, int) short. Rectum (figure 23, r) broad, thin-walled, voluminous. Rectal gland (figure 23, rg) spans dorsal, distal $\frac{1}{4}$ of rectum. Anus (figure 23, a) simple, pendant from wall of mantle cavity.

Female reproductive system: Ovary salmon colored, ascinous, lines adapical side of digestive gland. Oviduct (figure 24, od) thin, passes through kidney, runs along pericardial wall before joining pallial oviduct at juncture of albumen gland, capsule gland, and duct of ingesting gland. Albumen gland (figure 24, ag) short, laterally compressed, forms anterior portion of right wall of kidney. Ingesting gland (figure 24, ig) small, whitish, with long duct. Capsule gland (figure 24, cg) long, narrow, divided into proximal and distal regions by transverse ridge visible along outer wall as narrow, light colored band. Bursa copulatrix (figure 24, bc) ovate, abutts against capsule gland, laterally compressing its anterior end. Female opening (figure 24, fo) ventral slit along anteriormost end of bursa copulatrix.

Male reproductive system: Testis (figure 25, te) pale orange, situated along adapical side of digestive gland. Testicular duct (figure 25, td) runs anteriorly, expands and becomes convoluted, forming seminal vesicle (figure



Figures 23–26. Anatomical features of *Benthovoluta claydoni* new species. 23. Alimentary system. 24. Female pallial oviduct. 25. Male reproductive system. 26. Ventral view of penis tip.

a, anus; ag, albumen gland; bc, bursa copulatrix; bcv, buccal cavity; cg, capsule gland; dg, digestive gland; dgl, duct of gland of Leiblein; e, eye; fo, female opening; gl, gland of Leiblein; ig, ingesting gland; int, intestine; od, oviduct; p, proboscis; pe, posterior esophagus; pen, penis; r, rectum; rg, rectal gland; sg, salivary gland; sgr, sperm groove; sto, stomach; sv, seminal vesicle; t, tentacle; td, testicular duct; te, testis; vl, valve of Leiblein.

25, sv) along anterior portion of kidney and pericardium. Duct straightens, enters rear of mantle cavity and runs anteriorly along its wall, ventral to rectum, descending to floor of mantle cavity at midlength to form muscular, open groove (figure 25, sgr). Groove runs anteriorly to

base of long, dorsoventrally compressed, distally tapering penis (figure 25, pen), and along its inner lateral edge to the distal end, where it passes along the ventral surface and extends to tip of papilla (figure 26, pap), situated in a concavity at the outer distal edge of penis.

Kidney: Kidney large, with broad nephridial gland adjacent to pericardium and about 10 heavily pleated lamellae emanating from dorsal and lateral walls.

Etymology: This species honors Michael Claydon, of Port Hedland, Western Australia, who first brought it to my attention, and generously provided material for study.

Type locality: SW of Imperieuse Reef, Rowley Shoals, Western Australia, 18°05'S, 118°10'E, in 400–401 m, mud bottom.

Holotype: Western Australian Museum WAM 3252-83, ♂, length 84.7 mm.

Paratypes: Paratypes 1–2, National Museum of Natural History, Smithsonian Institution USNM 862217, paratypes 3–4, WAM 3252-83, all from the type locality; paratype 5, WAM 972-84, WNW of Lacepede Archipelago, Western Australia, 15°40.2'S, 120°37.3'E to 15°42.6'S, 120°34.6'E, in 500–504 m, soft bottom; paratype 6, WAM 977-84, W of Cape Leveque, Western Australia, 16°09.5'S, 120°08.8'E to 16°07.6'S, 120°10.0'E, in 600–596 m, soft bottom; paratype 7, WAM 990-84, W of Broome, Western Australia, 17°59'S, 118°11'E to 18°01'S, 118°08'E, in 530–560 m, soft bottom; paratype 8, WAM 1556-84, WNW of Lacepede Archipelago, Western Australia, 15°46.4'S, 120°39.9'E to 15°43.8'S, 120°39.8'E, in 446–450 m, soft bottom; paratype 9, WAM 1564-84, WNW of Lacepede Archipelago, Western Australia, 15°51.2'S, 120°44.3'E to 15°49.3'S, 120°45.3'E, in 350–348 m, soft bottom; paratype 10, WAM 1866-84, W of Lacepede Archipelago, 16°55.4'S, 119°52.3'E to 16°57.4'S, 119°46.4'E, in 436–448 m, soft bottom; paratypes 11–12, WAM 1908-84, W of Lacepede Archipelago, Western Australia, 16°57.4'S, 119°52'E to 16°55'S, 119°56'E, in 434–432 m, soft bottom; paratype 13, WAM 1160-85, W of Lacepede Archipelago, Western Australia, 16°55.2'S, 119°50.9'E to 16°56.3'S, 119°54.8'E, in 430–436 m, soft bottom; paratype 14, USNM 862218, NW of York Sound, Western Australia, 12°54.4'S, 123°00.2'E to 12°50.6'S, 123°00.4'E, in 452–462 m, soft bottom; paratype 15, WAM 1681-84, NW of Collier Bay, Western Australia, 13°44'S, 122°13.3'E to 13°22.3'S, 122°14.7'E, in 496–494 m, soft bottom; paratypes 16–17, USNM 845602, 30–60 miles SW of West Island, Rowley Shoals, Western Australia, 250–430 m; paratype 18, American Museum of Natural History, AMNH 221361, off Port Hedland, Western Australia, in 450 m.

Distribution: All specimens examined in this study were taken along the upper continental slope off northern Western Australia at depths of from 350 to 596 m. The mean station depth was 453 m ($n = 15$). Cernohorsky (1973) figured and described a single, male specimen of this new species [as *Benthovoluta hilgendorfi* (von Martens, 1897)] from the Celebes Sea, 25 miles east of Zamboanga, Philippines, in about 450 m.

Ecology: *Benthovoluta claydoni* occurs on mud and soft bottoms at depths from 350 to 596 m. Live collected specimens had a thin or worn periostracum, yet lacked

epizoans, suggesting that this species may be an infaunal burrower. Numerous repaired breaks in a majority of the specimens examined, indicate frequent, unsuccessful predation by crabs and/or fish. Contents of the alimentary systems of three individuals were examined, one stomach contained fragments of an amphipod carapace. No polychaete setae were found in the guts of any of these specimens.

Comparative remarks: *Benthovoluta claydoni* most closely resembles the Japonic *B. hilgendorfi* (von Martens, 1897), which can be distinguished from *B. claydoni* by its chestnut brown color, spiral sculpture of incised furrows, and more pronounced axial sculpture. *Benthovoluta krigei* has a narrower, more fusiform shell with more evenly convex whorls, weaker axial sculpture that gives the body whorl a finely cancellate appearance, is tan in color with two to three darker spiral bands, and lacks or has very weak columellar folds. *Benthovoluta gracilior* Rehder, 1967, from somewhat deeper waters (928 m) of the Sulu Sea, differs from this new species in being smaller and more fusiform, and in having stronger axial sculpture that is not limited to the early whorls.

DISCUSSION

The genus *Benthovoluta*, as restricted above, is limited to the continental slopes along the margins of the Indian and western Pacific oceans in the Recent fauna. Fossil records are limited to the Pliocene of Japan (Yokoyama, 1920; Taki & Oyama, 1954) and the late Miocene or early Pliocene of Okinawa (MacNeil, 1960), and are all from bathynetric or bathyal depths. Of the Okinawan fossil species, *Benthovoluta okinavensis* MacNeil, 1960 is here reassigned to the genus *Cyomesus* on the basis of its small size, short siphonal canal, absence of spiral sculpture, prominent axial ribs, and overall resemblance to *Cyomesus barthelowi* (Bartsch, 1942). However, the fragments illustrated as *Phenacoptygma* new species (MacNeil, 1960: pl. 9, figs. 4, 5), are referable to the genus *Benthovoluta*, and represent the oldest known record for the genus.

Phenetically deduced relationships between the species of *Benthovoluta* based on UPGMA and single linkage clustering using the data in table 7 are shown in figure 27. Both algorithms produced dendrograms with identical topologies. Closest relationships are between the eastern Indian-western Pacific species, which differ in geographic and (*B. hilgendorfi*-*B. claydoni*), or (*B. claydoni*-*B. gracilior*) bathymetric distributions. Several examples of similar bathymetric zonation have been reported in the bathyal turbinellid subfamily Columbariinae, along with the suggestion that such bathymetric speciation occurred as a result of sea level changes during the Cenozoic (Harasewych, 1986). In contrast to the zoogeographic patterns seen in the Columbariinae, where there is considerable divergence between Indian and Pacific ocean species, and close similarity between eastern and western Indian Ocean taxa (Harasewych, 1986), *Benthovoluta claydoni*, which occurs in comparable

depths, spans both oceans, ranging from off Western Australia to the Philippines.

Dendrograms showing UPGMA and single linkage clustering of the Recent genera included in Ptychatactinae, based shell and radular characters (table 8), are shown in figure 28. In each instance, the genera *Ceratoxancus* and *Latiromitra* are clustered together and differentiated from the other genera referred to Ptychatactinae. Although originally described in the family Turbinellidae, several authors have commented on the affinities of *Ceratoxancus* to the Mitridae (Sakurai, 1957) or Volutomitridae (Cernohorsky, 1973). The radulae and protoconchs of the two species in this genus are unknown. Prior to Bouchet and Waren's (1985) reassignment of *Latiromitra* to Ptychatactinae on the basis of overall conchological similarity to *Cyomesus*, this genus had been included in the families Buccinidae (Locard, 1897), Costellariidae (Thiele, 1929), and Volutomitridae (Cernohorsky, 1970). The radula of this monotypic genus is unknown. Bouchet and Waren (1985:255) commented on the multispiral protoconch of the type species, and suggested its larvae are planktotrophic. All members of the family Turbinellidae for which developmental data are available undergo direct development (Bandel, 1975a,b), and have large, bulbous, although occasionally multispiral, protoconchs (Vasinae—Abbott, 1959; Columbariinae—Darragh, 1969; Harasewych, 1983, 1986; Ptychatactinae—Bouchet & Waren, 1985; herein; Turbinellinae—Bandel, 1975b). Other than superficial conchological similarity, there is little evidence for inclusion of either of these genera in the family Turbinellidae. Determination of their true phylogenetic affinities will require anatomical and radular data.

The remaining genera have been referred to the Ptychatactinae on the basis of conchological as well as radular features. The close relationships between *Benthovoluta* and *Surculina* have been noted previously (Rehder, 1967; Kilburn, 1971). Although similar in shell morphology, these genera differ substantially in size (*Surculina* rarely exceeding 40 mm in length), bathymetric

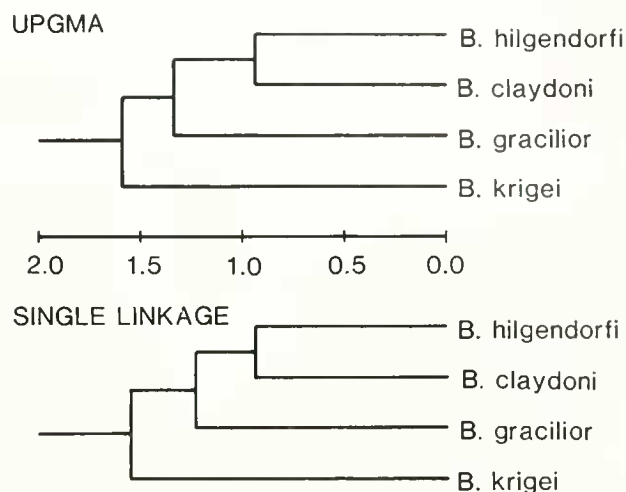


Figure 27. Phenetically deduced relationships between species in the genus *Benthovoluta*, produced by UPGMA (upper) and single linkage (lower) clustering of Euclidian distances between taxa, calculated using standardized data

distribution (with a single exception *Surculina* inhabit depths in excess of 1,000 m), and geographic distribution (*Surculina* are known only from New Zealand and the eastern Pacific). Dall (1908) reported that the animal of *S. cortezi* (Dall, 1908) lacked eyes, tentacles and operculum. Although the loss of eyes is not uncommon in deep water gastropods (Knudsen, 1973; Harasewych, 1987), the absence of tentacles and opercula in these animals is enigmatic.

Both clustering algorithms produced identical dendrograms of the relationships between the remaining small-shelled genera. *Cyomesus*, which is here regarded as distinct from *Latiromitra*, is the only Ptychatactine genus to have Recent representatives in the western Atlantic and western Pacific oceans. In his description of this genus, Quinn (1981:76) raised the possibility that the western Pacific representatives, which now include *Cyo-*

Table 7. Measurements of shell characters in the format mean/standard deviation. All linear measurements in mm. Mean values constitute the data matrix for phenetic analyses or relationships between *Benthovoluta* species.

Character	<i>hilgendorffi</i> n = 3	<i>claydoni</i> n = 5	<i>gracilior</i> n = 5	<i>krigei</i> n = 3
1) Sbc	2.75/0.01	2.88/0.10	2.63/0.17	3.24/0.11
2) Ssc	4.26/0.25	3.96/0.80	6.05/0.12	4.57/0.18
3) Rsl	0.68/0.06	0.68/0.04	0.99/0.11	0.70/0.10
4) beta	-1.6/1.4	-2.5/1.2	4.1/1.4	1.3/2.5
5) theta	12.2/2.2	11.5/1.4	11.9/0.6	11.4/0.3
6) W	1.38/0.02	1.49/0.03	1.47/0.01	1.58/0.05
7) D	0.18/0.04	0.22/0.04	0.17/0.00	0.15/0.05
8) T	7.64/0.36	7.50/0.47	5.43/0.55	9.14/0.67
9) A + SLC/SL	0.578/0.005	0.596/0.004	0.547/0.012	0.567/0.019
10) CP	0.0	0.0	0.0	1.0
11) C	1.0	0.0	0.0	1.0
12) Sut	0.0	0.0	0.0	1.0
13) Sculp	0.0	0.0	0.0	1.0

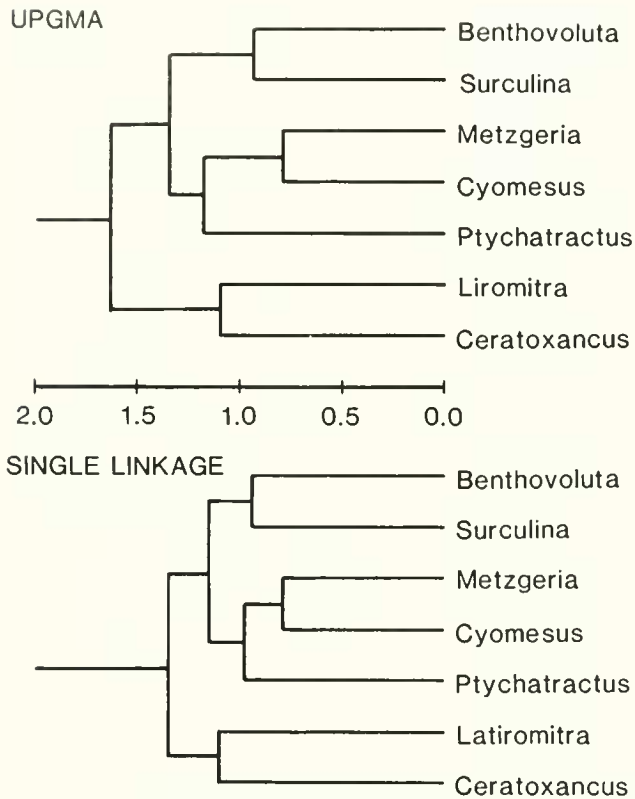


Figure 28. Phenetically deduced relationships between genera assigned to the subfamily *Ptychactrininae*, produced by UPGMA (upper) and single linkage (lower) clustering of Euclidian distances between taxa, calculated using standardized data.

mesus barthelowi (Bartsch, 1942), *C. delicatula* (Shikama, 1971), *C. sakashitai* (Habe, 1976), and *C. nakayasui* (Habe, 1976), might be separable into a separate subgenus. Most closely related to *Cyomesus*, or at least to its western Atlantic type species, is *Metzgeria*, from the bathyal zone of the northeastern Atlantic. These genera have very similar shell and radular morphologies as well as bathymetric ranges. Although several additional,

Table 9. Character state distributions of anatomical characters listed in table 5 among the subfamilies of Turbinellidae. COL = Columbariinae; PTY = Ptychactrininae; TUR = Turbinellinae; VAS = Vasinae.

Character	COL	PTY	TUR	VAS
1)	b	c	c	a
2)	a	a	b	a
3)	b	a	b	a
4)	b	b	b	a
5)	a	a	a	b
6)	a	a	a	b
7)	a	a	a	b
8)	a	a	b	a
9)	a	b	a	a
10)	a	b	b	a

geographically remote, species have been described in the genus *Metzgeria*, their generic assignments are considered either speculative (*M. californica* Dall, 1903; *M. montereyana* Smith and Gordon, 1948), being based on vague conchological similarities, or erroneous (*M. apodema* Bouchet and Talavera, 1981) by virtue of having a multispiral larval shell. More remotely related to both these taxa is *Ptychactrinus*, the type genus of the subfamily. Similar to both genera in size and shell morphology, it is characterized by prominent spiral sculpture and by a radula that has features of *Cyomesus* as well as of *Benthovoluta* (figure 19).

Although fossil representatives of most of the Recent genera are unknown, a number of Cretaceous and Eocene genera have been regarded as possible members of the Ptychactrininae (Quinn, 1981). Examination of several specimens of the type species of *Palcofusimitra* Sohl, 1963 and *Fusimitra* Conrad, 1855 revealed only superficial similarity in shell form with any member of the Ptychactrininae. The similarity of the single known specimen of the Cretaceous genus *Mitridomus* Sohl, 1963 to *Latiromitra* had been noted by Sohl, 1964; however, resolution of the question of whether *Mitridomus* rep-

Table 8. Measurements of shell characters used in phenetic assessment of the relationships of the Recent genera assigned to the subfamily Ptychactrininae. All linear measurements are in mm. BEN = *Benthovoluta*, CER = *Ceratoxancus*, CYO = *Cyomesus*, LAT = *Latiromitra*, MET = *Metzgeria*, PTY = *Ptychactrinus*, SUR = *Surculina*.

Character	BEN	CER	CYO	LAT	MET	PTY	SUR
1) Sbc	2.75	2.67	2.23	2.17	2.00	1.63	2.44
2) Ssc	4.26	2.02	2.71	2.00	2.78	2.23	3.11
3) Rsl	0.68	0.41	0.72	0.41	0.60	0.50	0.73
4) beta	-1.6	-16.3	-4.1	-13.5	-4.8	-11.2	-0.5
5) theta	12.2	18.5	16.1	10.2	16.0	18.8	11.4
6) W	1.35	1.49	1.42	1.51	1.73	1.69	1.67
7) D	0.18	0.32	0.15	0.27	0.15	0.18	0.19
8) T	7.64	5.36	6.94	5.93	6.25	5.35	5.99
9) A + SLC/SL	0.55	0.55	0.59	0.47	0.54	0.51	0.60
10) Prot	1.0	?	1.0	0.0	1.0	1.0	1.0
11) Lat	1.0	?	0.0	?	0.0	1.0	1.0
12) Rach1	1.0	?	0.0	?	0.0	1.0	1.0
13) Rach2	1.0	?	0.0	?	0.0	0.0	1.0

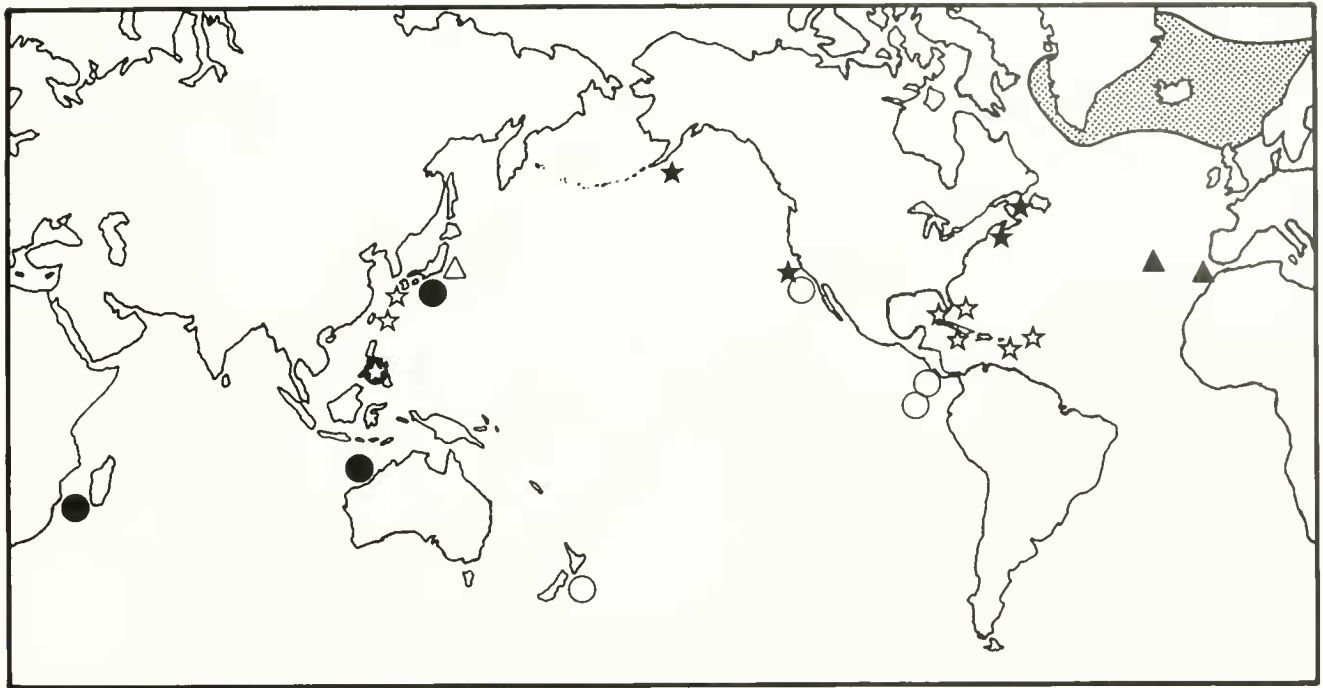


Figure 29. Recent geographic distribution of genera assigned to the subfamily Ptychactractinae. Open stars = *Cyomesus*; closed stars = *Ptychactractus*; open circles = *Surculina*; closed circles = *Benthovoluta*; open triangle = *Ceratoxancus*; closed triangles = *Latiromitra*; stippled area = *Metzgeria*.

resents an early ptychactractine, and *Latiromitra* a recent descendant that retained a multispiral protoconch, or whether both genera had previously been correctly assigned to the family Mitridae, must await the availability of anatomical material of *Latiromitra*. Several species of the genus *Mesorhytis* Meek, 1876 from the Upper Cretaceous of the United States bear strong resemblance to Recent *Benthovoluta*, although they are smaller in size (about 30 mm). *Mesorhytis dakotaensis* Stanton, 1920 from Paleocene deposits of North Dakota, more closely resembles *Cyomesus*, and had a paucispiral protoconch. "*Fasciolaria*" *assimilis* Stoliczka, 1868 from the Upper Cretaceous of southern India, bears unmistakable resemblance to Recent species of *Benthovoluta*, and had attained a size of 140 mm. As inclusion of even Recent species in the Ptychactractinae on purely conchological characters is uncertain, the assignment of Cretaceous genera to this group must remain tentative.

The geographic distribution of the Recent genera of Ptychactractinae (figure 29) indicates that, with the single exception of *Latiromitra*, a monotypic genus with planktonic larvae questionably included in Ptychactractinae, all are restricted to continental margins or their adjacent abyssal plains. The distribution of the genus *Surculina* indicates that this group evolved in the Austral Province (Kauffman, 1973), prior to the separation of New Zealand at the end of the Early Paleocene, and is an offshoot of east Tethyan *Benthovoluta* or its precursors. The closing of the Tethys Sea at the end of the Eocene separated the Atlantic and Pacific species of the genus *Cyomesus*. The close resemblance of *Metzgeria* to the western Atlantic

type species of *Cyomesus* suggests that *Metzgeria* is an offshoot from the west Tethyan branch of that genus. The origin of the genus *Ptychactractus* is more obscure. One possibility is that it diverged from the east Tethyan (western Pacific) branch of *Cyomesus*, evolved in the northern Pacific, with one branch extending southward along the western coast of North America, while another was part of the late Pliocene Beringean Transgression of Pacific boreal mollusks through the Bering Strait, across the Arctic, and into the North Atlantic (Durham & MacNeil, 1967; Nelson, 1978). The relationship of *Latiromitra* to the Cretaceous *Mitridomus* has been discussed previously. The affinities of *Ceratoxancus* are uncertain. If it is indeed a ptychactractine, it may be an offshoot of any of the equally questionable, mitriform, Cretaceous turbinellids.

Dissections of *Benthovoluta claydoni* new species revealed a basically turbinellid anatomical organization that most closely resembled *Turbinella angulata* in most features of the shell, mantle cavity, and alimentary and male reproductive systems, and *Coluzea rotunda* in features of the female reproductive system. The short muscular proboscis and torted, papillate penis, also found in *Cyomesus chaunax*, distinguish these taxa from all other turbinellids, and may prove to be diagnostic of the subfamily Ptychactractinae. The presence of an amphipod carapace in one stomach, as well as an absence of polychaete setae from the guts of all three of the specimens examined, suggest a diet different from that reported for the other subfamilies within Turbinellidae.

The phylogenetic relationships of the four subfamilies

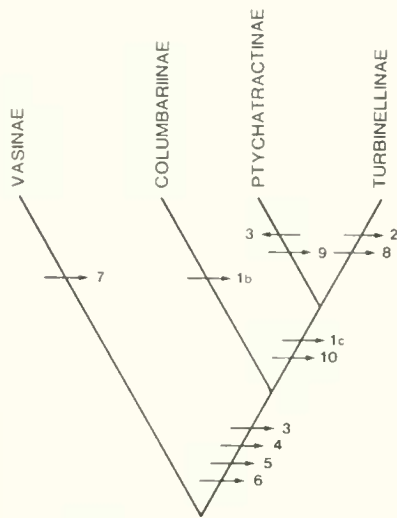


Figure 30. Cladograms indicating the relationships between the subfamilies of the family Turbinellidae, based on characters in table 5.

of Turbinellidae, as deduced from an analysis of the taxa in table 4 scored for the characters in table 5, are shown by the cladogram in figure 30. This cladogram, with a consistency index of 0.917, indicates that the subfamily Ptychatractinae is most closely related to the Turbinellinae, and that divergence between the Vasiniae and the remaining subfamilies is the most ancient. This phylogenetic arrangement is at least partially supported by the fossil record, as the subfamilies Vasiniae, Columbariinae, and Ptychatractinae all have Cretaceous representatives (Wenz, 1943; Darragh, 1969; herein), while earliest records of Turbinellinae date from the Lower Eocene (Vokes, 1964).

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